Life History and Ecology of the Humpback Chub in the Colorado River in Grand Canyon, Arizona

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Abstract. The endangered humpback chub (*Gila cypha*) is found as six populations in the Colorado River Basin. The largest is in Grand Canyon, Arizona, where in 1990–1993, fish were distributed as nine aggregations in 307 km of the Colorado River, as well as in the lower 14.9 km of the Little Colorado River (LCR), a seasonally-warmed tributary. An estimated 3,700 adults inhabited the mainstem in 1993, with 3,480 adults in the largest aggregation near the LCR. The LCR was the only area with significant spawning and recruitment of fish to the mainstem, but it was used only by the nearby mainstem aggregation and a resident LCR population. Year-round releases of 8–10°C water from Glen Canyon Dam precluded successful mainstem reproduction and limited growth of young chubs. Adults exhibited a high degree of spatial fidelity for specific river locales; mean net movement was 1.49 km (range = 0–6.11; SD = 1.50) for 69 radio-tagged fish and 1.64 km (range = 0–99.8; SD = 1.72) for 238 Passive Integrated Transponders (PIT)-tagged fish. Annual survival of chubs during the first 3 years of life was estimated at 0.10, while estimated annual survival of adults (age 3+) was 0.93. A major source of subadult mortality was predation by brown trout (*Salmo trutta*) and channel catfish (*Ictalurus punctatus*), which together potentially consumed about 228,850 chubs annually. Adult chubs inhabited primarily large recirculating eddies (88% captures, 74% radio contacts), whereas subadults used shorelines with vegetation, talus, and debris fans, as well as eddy return channels (i.e., backwaters). Diet by volume of mainstem adults near the LCR consisted of *Gammarus lacustris* (freshwater amphipods, 45%), Simuliidae (blackflies, 40%), terrestrial invertebrates (9%), Chironomidae (midges, 5%), and other aquatic invertebrates (1%). Adults from more downstream aggregations consumed a lower proportion of *G. lacustris* and a higher proportion of terrestrial invertebrates. External parasitic copepods (*Lernaea cyprinacea*) were on 8 of 6,294 (<1%) chubs examined and Asian tapeworms (*Bothriocephalus acheilognathi*) were in guts of 6 of 168 (4%) adults flushed with a stomach pump.

Key words: Annual survival, Colorado River, diet, endangered species, *Gila cypha*, Grand Canyon National Park, humpback chub, parasites, predation, reproduction.

The humpback chub (*Gila cypha*) is a large river cyprinid fish that inhabits canyon reaches of the Colorado River Basin (Fig. 1). This indigenous species has declined throughout its range as a result of dam construction, flow modifications, changes in water chemistry, and introduction of competing and predaceous nonnative fishes (Valdez and Clemmer 1982). The humpback chub was included in the first List of Endangered Species on 11 March 1967 (32 FR 4001) and currently remains protected by the Endangered Species Act of 1973, as amended.

Investigations funded by the Bureau of Reclamation, through the Glen Canyon Environmental Studies (GCES) Phase I, 1983–1988, reported that construction of Glen Canyon Dam and subsequent operation jeopardized continued existence of the humpback chub in Grand Canyon through regulated releases of cold hypolimnetic waters (U.S. Department of the Interior 1988). The present study, conducted under GCES Phase II, 1988–1996, was designed to describe physical, chemical, and biological components of the mainstem Colorado River and identify and quantify principal factors limiting the survival of humpback chub in Grand Canyon. The study evaluated life history attributes, including distribution, abundance, movement, reproduction, age and growth, survival, habitat, food habits, predation, and parasites; detailed results were presented in a final project report (Valdez and Ryel 1995). Concurrent, cooperative studies were conducted on the mainstem and tributaries by Arizona Game and Fish Department (1996), Arizona State University (McElroy and Douglas 1995, Douglas and Marsh 1996), and U.S. Fish and Wildlife Service (1994).

Study Area and Methods

The study was conducted in 364 km of the Colorado River in Grand Canyon, Arizona (Fig. 2). Sampling was conducted monthly from October 1990 through November 1993 from Lees Ferry to Diamond Creek. Four study regions were divided longitudinally into 11 geomorphic reaches, previously designated by Schmidt and Graf (1988), and a stratified random design was implemented to sample fish assemblages and associated physical, chemical, and biological components (Valdez and Ryel 1995). Sampling was also partitioned by season for winter (December–February), spring (March–May), summer (June–August), and fall (September–November), and by day, night, dawn, and dusk. Since day length and photoperiod varied with season, a computer program (Sun and Moon Events Worksheet, Heizer Software, Inc.,

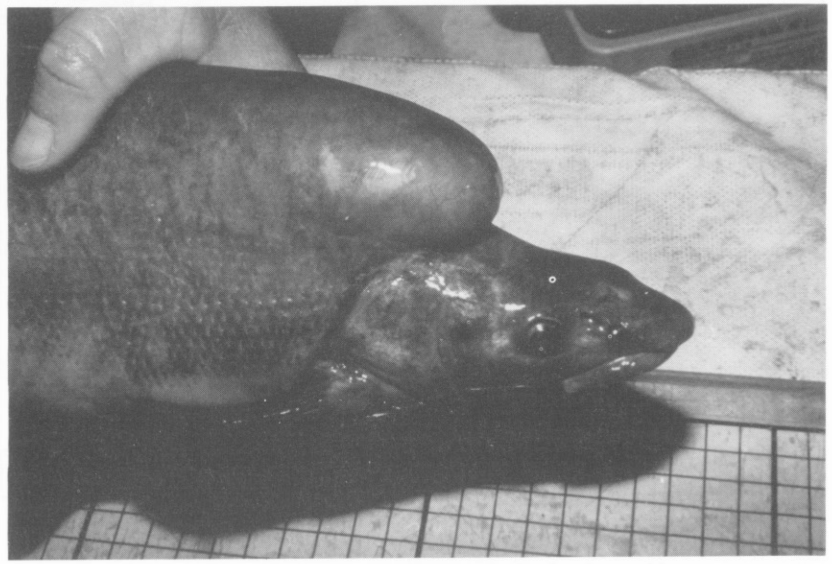


Fig. 1. Adult female humpback chub captured 72 km downstream of Glen Canyon Dam on 15 July 1995. Total length = 480 mm, weight = 1,165 g.

Palo Alto, California) was used to appropriately adjust time blocks. Landmarks in this paper are presented by river kilometer (RK) or distance downstream from Lees Ferry, which is 25.4 km downstream of Glen Canyon Dam.

Fish were sampled with five gear types, including gill and trammel nets, electrofishing, minnow traps, hoop nets, and seines, as described by Valdez et al. (1993). Gill and trammel nets were used to sample large fish in deep habitats; these are standard gears used to survey and monitor other populations of humpback chub in the Upper Colorado River Basin (McAda et al. 1994). Electrofishing was used to sample fish within distinct shoreline types (i.e., vegetation, talus, debris fan, bedrock, cobble bar, sand bar) to evaluate habitat use and reduce variance of catch statistics. Electrofishing was conducted from an Achilles SU-16 research boat with current supplied by a 5000-W generator and routed through a Mark XX Complex Pulse System (CPS) to stainless steel spherical electrodes. Unbaited minnow traps, set in pods of five as replicates, were used to sample the same shoreline types described for electrofishing. Three sizes of winged hoop nets (hoop diameters of 0.6, 0.9, and 1.2 m) were used in shoreline constrictions or at the mouths of backwaters. Two mesh sizes of seines (0.6 and 0.3 cm square mesh) were

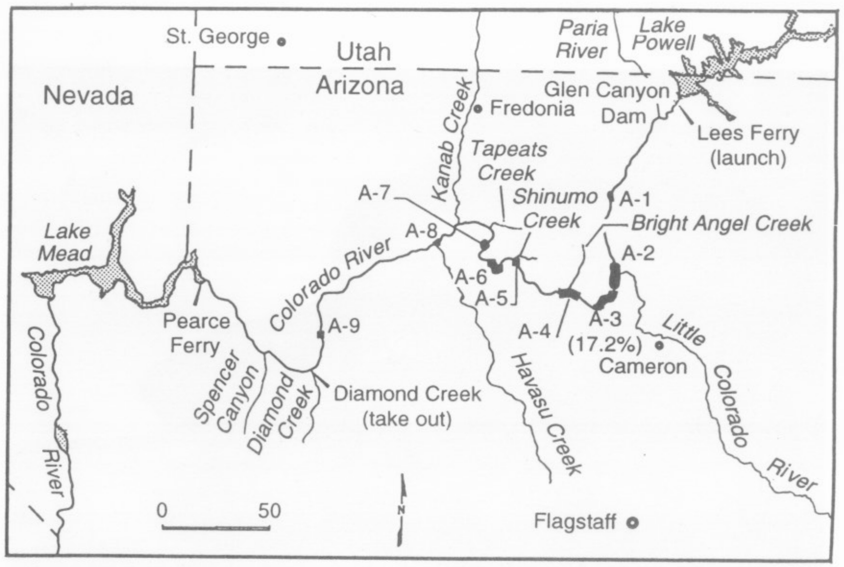


Fig. 2. Study area of the Colorado River in Grand Canyon, Arizona. Nine aggregations of humpback chubs are shown as numbered shaded areas (A-1 to A-9).

used to sample assemblages of small fish in habitats up to about 1.5 m deep. Catch per unit effort (CPUE) was computed for each sample and averaged for stated data partitions.

Humpback chubs were measured for total length (TL), standard length (SL), and forked length (FL) in millimeters, weighed wet in grams, and examined for gender. A nonlethal stomach pump (Wasowicz and Valdez 1994) was used on 168 adults (>250 mm TL) to flush gut contents and evaluate food habits. Scales were taken from chubs smaller than 200 mm TL to determine age and size at which fish moved from the warm Little Colorado River (LCR) to the colder mainstem. Chubs between 60 and 150 mm TL were group-marked with fin-punch combinations, using a 3-mm diameter biopsy needle (Wydoski and Emery 1983), to track longitudinal dispersal of juveniles among subreaches.

Seventy-five adult humpback chubs were surgically equipped with radio transmitters, as described by Tyus (1982), Valdez and Nilson (1982), and Kaeding et al. (1990). Transmitters weighing 9 g (Advanced Telemetry Systems, ATS Model 1 BEI 10-18, battery life of 50 days) were implanted in fish weighing 450–549 g, and transmitters weighing 11 g (ATS Model 2 BEI 10-35, battery life of 75–120 days) were implanted in fish weighing 550 g or more, such that transmitter air weight did not exceed 2% of live fish weight

The transmitters emitted radio signals in the frequency range of 40.600 to 40.740 MHZ at rates of 40, 60, or 80 pulses/min. Movements of these fish were monitored with ATS Model R2000 and Smith-Root Model SR-40 receivers, and were described as net movement (distance between first and last contact points) and gross movement (sum of distances moved between all contact points).

All other fish were measured for TL and SL, weighed, examined for reproductive condition and gender, and released. Selected numbers of brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), channel catfish (*Ictalurus punctatus*), and striped bass (*Morone saxatilis*) were sacrificed and examined for food habits and evidence of predation on native species. All native fishes 150 mm TL or larger were marked with PIT (Passive Integrated Transponders) tags, which were injected into the peritoneal cavity of each fish (Burdick and Hamman 1993).

Results and Discussion

Distribution and Abundance

The first description and photographic documentation of the humpback chub ("bony tail") in the Colorado River in Grand Canyon was by Kolb and Kolb (1914) in 1908 from the LCR near Beamer's Cabin, about 200 m upstream from the outflow (Fig. 3):

> "On the opposite side of the pool the fins and tails of numerous fish could be seen above the water. The striking of their tails had caused the noise we had heard. The `bony tail' were spawning. We had hooks and lines in our packs, and caught all we cared to use that evening."

The species was described in 1945 by Miller (1946) from three partial specimens believed caught near Bright Angel Creek in Grand Canyon. The earliest catalogued collections of humpback chub and two congeneric species from several locations in Grand Canyon were also by Miller in the 1940s. The 27 specimens are held at the University of Michigan fish collection and include 5 humpback chub, 16 bonytail (*G. elegans*), and 6 roundtail chub (*G. robusta*); these specimens were described morphologically and meristically by Bookstein et al. (1985). Also, Wallis reported eight juvenile humpback chubs from Spencer Creek in 1950 (Kubly 1990). These few historic records show the species was in and near tributary inflows in Grand Canyon, with large numbers reported in the lower LCR, probably during a spawning aggregation. Humpback chubs were also likely in many mainstem areas, based on current distribution and habitat used by upper basin populations (Valdez et al. 1990). Following completion of Glen Canyon Dam in 1963,

Fig. 3. Aerial view of the Little Colorado River (from upper left) flowing into the Colorado River (left to right) in Grand Canyon, 124 km downstream of Glen Canyon Dam.

humpback chubs were commonly reported in Arizona Game and Fish Department creel census from the Colorado River near Lees Ferry during 1963–1967 (Stone 1964, 1966, Stone and Queenan 1967), but sampling of seven major tributaries (excluding the LCR) between Lees Ferry and Lake Mead in 1968 yielded none (Stone and Rathbun 1968). Holden (1973) collected 15 humpback chubs in July 1967 and 1 in August 1970, all within a few hundred meters downstream of Glen Canyon Dam. Humpback chub have not been captured within 31 km of the dam since 1970 (Carothers and Minckley 1981), which was about the time Lake Powell stratified and cold water releases began to persist year-round (Stanford and Ward 1991). Humpback chubs could have been excluded from the tailwater by these cold releases, by high floods in 1983–1984, or by predation from large rainbow trout weighing up to 7 kg (Carothers and Brown 1991).

From 1970 through 1976, Suttkus and Clemmer (1977) reported young-of-year (YOY) and juvenile humpback chubs between President Harding Rapid (RK 71) and Shinumo Creek (RK 174). Researchers from the Museum of Northern Arizona (Carothers and Minckley 1981) also captured chubs during six river trips in 1977–1979, including adults between North Canyon (RK 31) and Boulder Wash (RK 312), and one juvenile (<100 mm TL) just above Granite Rapid (RK 150). Of 19 tributaries sampled from the Paria River (RK 1.4) to Travertine Creek (RK 369), humpback chubs were captured only in the LCR.

From 1980 through 1981, biologists from FWS captured 504 adult humpback chubs between Nankoweap Canyon (RK 84) and Unkar Rapid (RK 116) (Kaeding and Zimmerman 1983). Fish abundance was reported to resemble a normal or "bell-shaped" distribution with greatest numbers near the LCR inflow. Chubs smaller than 145 mm TL were not caught in the Colorado River above the LCR inflow, although many small specimens were caught in spring and fall below the inflow, providing the first evidence that post-dam chub reproduction was occurring primarily in the LCR. From 1984 through 1989, Arizona Game and Fish Department (Maddux et al. 1987, Kubly 1990) reported humpback chubs in the Colorado River from South Canyon (RK 51) to RK 349, mostly in or near the LCR (RK 99). Ninety-six percent of chubs captured were between RK 51 and RK 140, and specimens were also captured at the inflows of four tributaries, including Bright Angel, Shinumo, Kanab, and Havasu creeks, but not in the tributaries themselves.

The present study, 1990–1993, reported 15 species of fish in the Colorado River between Lees Ferry and Diamond Creek, including 4 native or indigenous species and 11 nonnative or exotic species (Table 1). Humpback chubs were targeted in sampling and were the second most common fish captured with 22% of total catch. The chubs occurred as nine aggregations (Fig. 2; Table 2) in 307 km (from above South Canyon [RK 48] to Granite Springs Canyon [RK 355]), as well as a resident population in the lower 14.9 km of the LCR (Douglas and Marsh 1996). The nine aggregations accounted for 94% of all humpback chubs captured in the mainstem (5,940 of 6,294), or 92% of YOY (2,640 of 2,865), 94% of juveniles (1,545 of 1,638), and 98% of adults (1,755 of 1,791). Total numbers of adults in these aggregations ranged from 5 to 3,482 for a total of about 3,700, based on population estimates in 1993 (Valdez and Ryel 1995). Adults in these aggregations had a high recapture rate, indicating long-term residence and no significant exchange of individuals among aggregations. In a separate study (Valdez et al. 1994), one adult female humpback chub was caught on 5 October 1993 near Maxon Canyon (RK 407) about 44 km downstream of Diamond Creek.

The present distribution of humpback chubs in Grand Canyon shows fish near seasonally-warmed tributary inflows, warm springs, and in reaches with a high frequency of large recirculating eddies formed by debris fans. Historic and recent records, as well as recent life history information, indicate the distribution and abundance of humpback chubs in the Colorado River in Grand Canyon have been reduced. This reduction probably began before Glen Canyon Dam in 1963, as a result of regional land use practices, degraded water quality, and introduction of nonnative fishes (Miller 1961). We estimate 30% loss in distribution of humpback chubs in 364 km of the Colorado River included in this study, primarily as a result of cold dam releases, which limit

Table 1. Fish species captured in the Colorado River from Lees Ferry to Diamond Creek, October 1990 to November 1993.

Common and scientific name	Species code	Status[a]	Young-of-year	Juvenile	Adult	Total	Percent
Family: Cyprinidae (minnows)							
Common carp (*Cyprinus carpio*)	CP	EX	4	44	2,375	2,423	8.6
Humpback chub (*Gila cypha*)	HB	EN	2,865	1,638	1,791	6,294	22.3
Fathead minnow (*Pimephales promelas*)	FH	NN	44	12	1,074	1,130	4.0
Speckled dace (*Rhinichthys osculus*)	SD	NA	4	92	1,395	1,491	5.3
Family: Catostomidae (suckers)							
Bluehead sucker (*Catostomus discobolus*)	BH	NA	101	250	689	1,040	3.7
Flannelmouth sucker (*Catostomus latipinnis*)	FM	EN	183	395	2,197	2,775	9.8
Flannelmouth x Razorback sucker	FR	-	0	0	5	5	<0.1
Unidentified sucker	SU	-	32	0	0	32	0.1
Family: Ictaluridae (catfishes, bullheads)							
Black bullhead (*Ameiurus melas*)	BB	NN	0	3	3	6	<0.1
Channel catfish (*Ictalurus punctatus*)	CC	NN	4	5	104	113	0.4
Family: Salmonidae (trout)							
Rainbow trout (*Oncorhynchus mykiss*)	RB	NN	169	1,152	9,800	11,121	39.4
Brown trout (*Salmo trutta*)	BR	EX	2	107	1,564	1,673	5.9
Brook trout (*Salvelinus fontinalis*)	BK	NN	0	0	6	6	<0.1

Table 1. *Concluded.*

Common and scientific name	Species code	Status[a]	Young-of-year	Juvenile	Adult	Total	Percent
Family: Cyprinodontidae (killifishes)							
Plains killifish (*Fundulus zebrinus*)	PK[b]	NN	1	0	75	76	0.3
Family: Percichthyidae (temperate basses)							
Striped bass (*Morone saxatilis*)	SB	NN	0	0	39	39	0.1
Family: Centrarchidae (sunfish)							
Green sunfish (*Lepomis cyanellus*)	GS	NN	1	1	1	3	<0.1
Family: Percidae (perches)							
Walleye (*Stizostedion vitreum*)	WE	NN	0	0	1	1	<0.1
Totals			3,410	3,699	21,119	28,228	100

[a]NA = native to the drainage.
EN = endemic to the drainage.
EX = exotic, introduced from another continent.
NN = non-native, introduced from another drainage in North America.

[b]Common synonym Rio Grande killifish.

Table 2. Location and numbers of humpback chub in nine aggregations, 1990–1993.

Aggregations	Location (RK)	Number captured			Estimated number of adults[a]
		Young-of-year	Juvenile	Adult	
A-1. 30-Mile	48–50	14	0	26	52
A-2. LCR Inflow	92–105	1,830	1,293	1,524	3,482
A-3. Lava to Hance	106–123	778	226	15	ne
A-4. Bright Angel Inflow	135–148	13	2	9	ne
A-5. Shinumo Inflow	174–175	4	13	27	57
A-6. Stephen Aisle	185–193	0	7	7	ne
A-7. Middle Granite Gorge	203–208	1	4	124	98
A-8. Havasu Inflow	251–252	0	0	7	13
A-9. Pumpkin Spring	342–343	0	0	6	5
Total		2,640	1,545	1,755	3,707

[a]Based on population estimates by Ryel and Valdez (1996).

[b]ne = no estimate because of insufficient recaptures.

reproduction, reduce food supplies, and maintain populations of large coldwater predators (i.e., trout). We also conclude an inferred reduction in abundance of chubs because of limited mainstem reproduction and survival, but the absence of historic estimates precludes assessing the magnitude of reduction. Assimilation of literature on humpback chub (Minckley 1996) reveals collections after about 1980 indicate distribution of the species has not changed dramatically in the last 13 years. Density estimates for the mainstem are not available to quantify changes in abundance, although Douglas and Marsh (1996) showed a decrease in adults in the LCR over the last decade.

Movement

Radio-tagged adult humpback chubs (>350 mm TL) moved relatively little during this study, suggesting strong fidelity to specific mainstem locales. Of 69 fish tracked for an average of 93 days (range = 30–170) near the mouth of the LCR (RK 92-105), mean net movement (Fig. 4a) was 1.49 km (range = 0.00–6.11; SD = 1.50), while mean gross movement was 5.13 km (range = 0.32–16.93; SD = 3.27). Spawning-related movements into and from the LCR were not included in this analysis. PIT-tagged chubs (≥150 mm TL) exhibited similar average net movement (Fig. 4b) of 1.64 km (range = 0.0–99.8; SD = 1.72) for consecutive captures separated by 1 to 1,065 days (238 fish, 285 movements). Movements of PIT-tagged fish were equally divided between upstream and downstream directions, with 85% of net movements less than 2 km. Net movements were not significantly different (t = 1.66, P = 0.098, df = 192) between males (n = 102; mean = 0.89 km; range = 0.0–4.9) and females (n = 92; mean = 1.22 km; range = 0.0–8.9), or between 238 PIT-tagged fish and 69 radio-tagged fish (t = 0.17, P = 0.867, df = 352). Movement of humpback chubs in Grand Canyon was similar to that reported for the species in Black Rocks, Colorado River, Colorado, where mean net movement was 0.8 km (range = 0–3.7) for 8 radio-tagged adults and 1.6 km (range = 0–23.0) for 16 Carlin-tagged adults (Valdez and Clemmer 1982). Kaeding et al. (1990) reported mean displacement for 30 radio-tagged adults of 0.8 km (range = 0–8.4; SD = 0.4) for the same area.

Although movement in the Colorado River in Grand Canyon was similar to that in Black Rocks, annual spawning-related movements of 419 PIT-tagged adults between the Colorado River and LCR resulted in a higher mean net movement of 6.4 km (range = 0.10–20.0; SD = 5.9), with means of 2.0 km (range = 0.0–6.5; SD = 1.6) in the mainstem and 4.4 km (range = 0.0–14.9; SD = 3.8) in the LCR. These fish were recaptured up to 14.9 km up the LCR, with 44% more than 3 km and 36% more than 5 km from the mouth (Fig. 5). Mean net movement was not significantly different between males (6.5 km) and females (5.8 km) (n = 372; t = 1.41; P = 0.075 df = 370). Net movements of PIT-tagged fish captured by Arizona State University in the LCR and recaptured by us in the mainstem were similar.

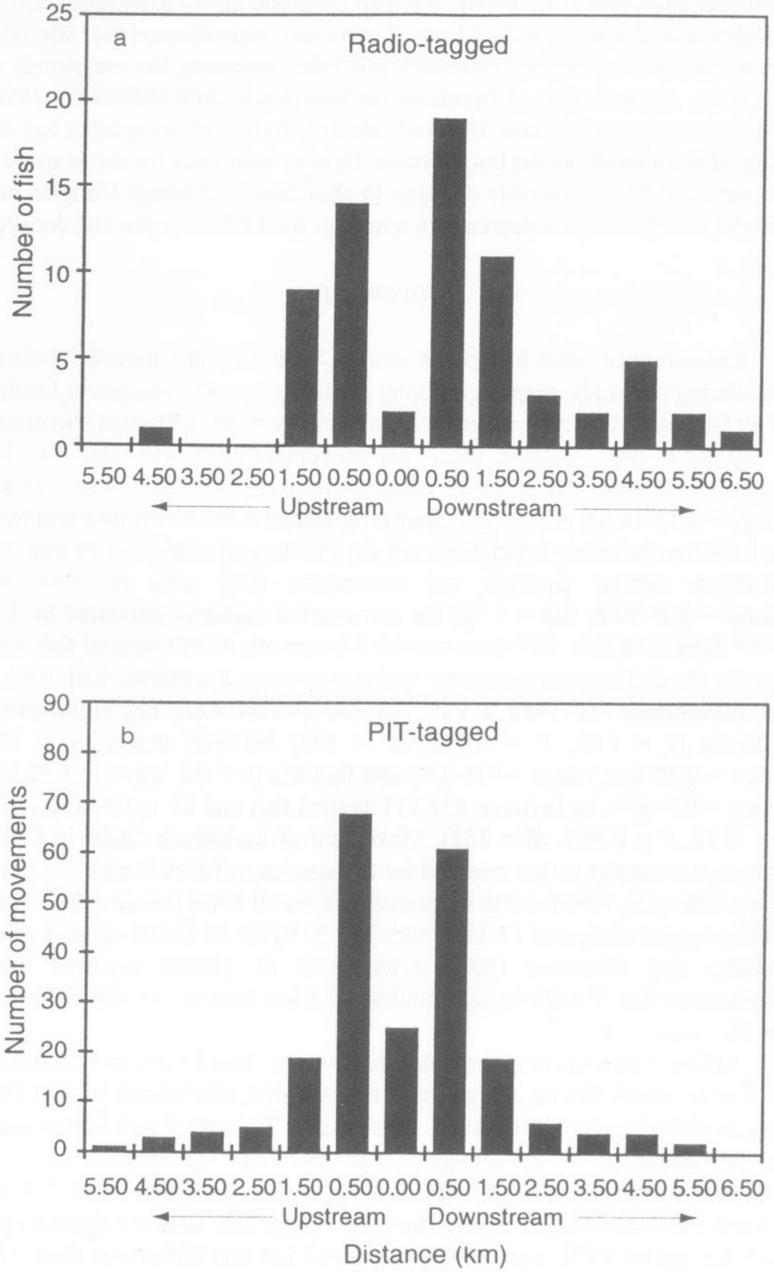


Fig. 4. Net movements of 69 radio-tagged adult humpback chubs (a) and 238 PIT-tagged adults (285 movements) (b) in the Colorado River, October 1990 through November 1993.

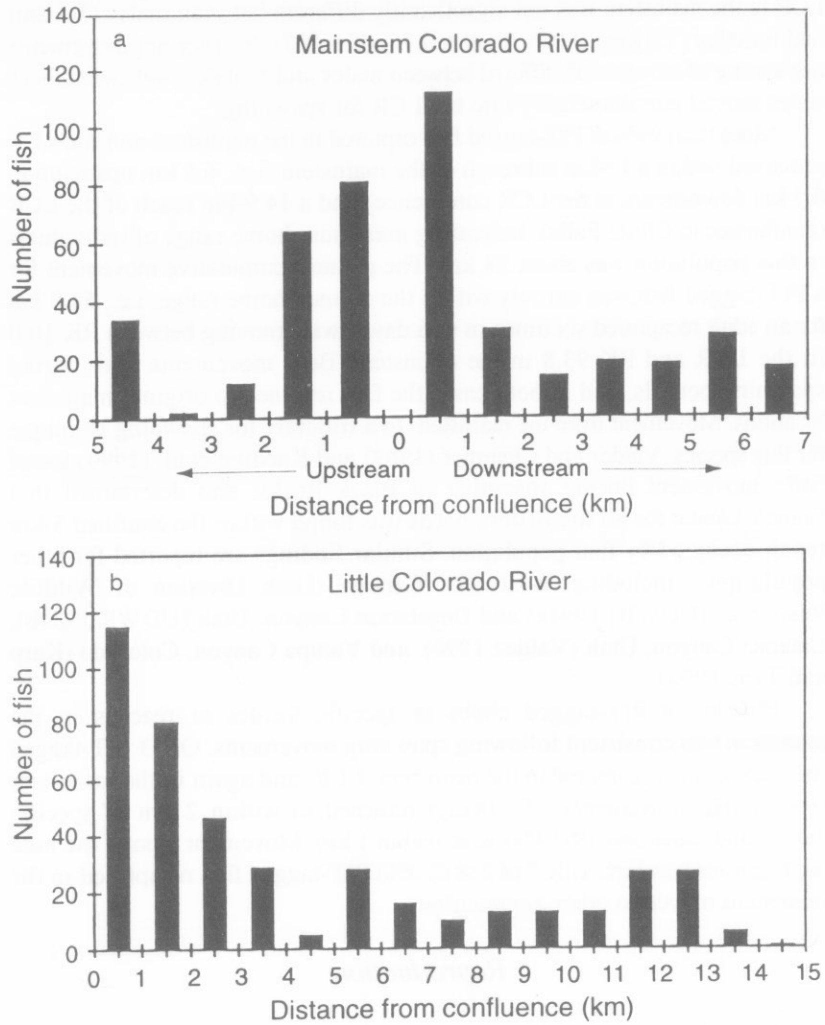


Fig. 5. Capture locations in the mainstem Colorado River (a) and recapture locations in the Little Colorado River (LCR) (b) for 419 PIT-tagged adult humpback chubs, October 1990 through November 1993. LCR recapture courtesy of M. E. Douglas and P. C. Marsh, Arizona State University.

Fish captured between RK 0 and RK 14.9 in the LCR were recaptured in the mainstem up to 4.9 km upstream and 24.2 km downstream of the LCR confluence (RK 94-123). Mean net movement of 401 fish (415 movements) from the LCR to the mainstem was 7.2 km (range = 0.08–34.10; SD = 6.8), with means of 5.3 km (range = 0.0–14.9; SD = 4.9) in the LCR and 1.9 km (range = 0.0–24.2; SD = 2.1) in the mainstem. Mean net movement from the

LCR to the mainstem was not significantly different between males (7.4 km) and females (7.2 km) ($t = 0.30$, $P = 0.76$, df = 357). Neither net movements nor timing of movements differed between males and females, indicating both sexes moved simultaneously into the LCR for spawning.

More than 99% of PIT-tagged fish captured in the mainstem and the LCR remained within a 13-km subreach of the mainstem (i.e., 6.5 km upstream to 6.5 km downstream of the LCR confluence) and a 14.9-km reach of the LCR (confluence to Chute Falls), indicating maximum home range of individuals in this population was about 28 km. The greatest cumulative movement for a PIT-tagged fish was entirely within the defined home range, i.e., 54.9 km for an adult recaptured six times in 626 days, twice moving between RK 10.0 in the LCR and RK 93.8 in the mainstem. Both movements were during spawning periods, and in both cases the fish returned to original mainstem locations. Movement from the mainstem to a tributary for spawning is unique for this species. Valdez and Clemmer (1982) and Kaeding et al. (1990) found little movement during spawning in Black Rocks, and determined that suitable habitat for all life history needs was found within the confined 5-km reach occupied by that population. Similar findings are reported for other populations, including Westwater Canyon (Utah Division of Wildlife Resources [UDWR] 1994a) and Desolation Canyon, Utah (UDWR 1994b), Cataract Canyon, Utah (Valdez 1990), and Yampa Canyon, Colorado (Karp and Tyus 1990).

Fidelity of PIT-tagged chubs to specific locales or reaches in the mainstem was consistent following spawning movements. Of 73 PIT-tagged fish consecutively captured in the mainstem, LCR, and again in the mainstem (round trip movements), 59 (81%) returned to within 2 km of specific mainstem locales and 38 (64%) were within 1 km. Movement among the nine aggregations was rare; only 7 of 238 (2.9%) PIT-tagged fish recaptured in the mainstem moved to other aggregations.

Reproduction

Overall male to female ratio of humpback chub in Grand Canyon was 49:51. Most successful spawning during this study occurred in the LCR by mainstem fish from the vicinity of the LCR, as well as by LCR residents. Successful mainstem spawning was precluded by cold dam releases, although evidence of reproduction (i.e., YOY) was found in warm shoreline springs about 48 km upstream of the LCR. Kaeding and Zimmerman (1983) found that, despite nearly constant mainstem temperatures, peak gonadal maturation of fish near the LCR inflow occurred in spring. We found that, of 178 adult chubs from the mainstem near the LCR during 1990–1993, peak spawning characteristics (i.e., expression of milt or eggs, tubercles, coloration) occurred in March, while 48 mainstem adults from other aggregations peaked in May, nearly 2 months later. These mainstem adults were from Middle Granite Gorge (RK 204–217; $n = 23$), near South Canyon (RK 48; $n = 7$), and inflows of Clear Creek (RK 135; $n = 4$), Bright Angel Creek (RK 141; $n = 1$), Shinumo Creek (RK 175; $n = 5$), and Havasu Creek (RK 252; $n = 5$). Ripe fish were captured in the mainstem from March through July at maximum water temperatures of 10–14°C, a range marginal for survival of eggs and larvae of humpback chub (Hamman 1982). Hatching success under laboratory conditions was 12%, 62%, 84%, and 79% at 12–13°C, 16–17°C, 19–20°C, and 21–22°C, respectively, while survival of larvae was 15%, 91%, 95%, and 99%, respectively (Hamman 1982). Marsh (1985) found similar relationships of temperature and survival. Despite the presence of ripe fish near tributaries, eggs and larvae were not found in inflows. Past investigators reported spawning by humpback chubs in the LCR in March, April, and May at water temperatures of 16–20°C (Suttkus and Clemmer 1977, Carothers and Minckley 1981, Kaeding and Zimmerman 1983).

These results suggest mainstem fish away from the seasonally-warmed LCR continue to achieve reproductive condition at about the same time as other populations in the basin (Valdez and Clemmer 1982), despite relatively constant river temperatures. Chubs in spawning condition were reported in Cataract Canyon, Utah at water temperatures of 16°C in June 1988 (Valdez and Williams 1993), and in Black Rocks at 11.5°C in June 1980 (Valdez and Clemmer 1982) and at 13–17°C in June 1983 and 15–23°C in July 1984 (Kaeding et al. 1990).

Although we found no evidence of spawning by humpback chubs in tributary inflows, reproduction was associated with a warm shoreline spring near RK 48. On 12 July 1994, about 100 YOY chubs were sighted among boulders in the warm plume and 14 voucher specimens (18–31 mm TL) were collected. Water temperature at the spring source was constant at 21.5°C, compared to 11°C in the adjacent mainstem. We believe these young fish hatched from eggs deposited in the warm spring plume, since mainstem water temperatures were too cold for survival of eggs or larvae (Hamman 1982, Marsh 1985). Based on average length of 24 mm TL (20 mm SL), these young were hatched about 8 June 1994 and were approximately 36 days old (D), as determined by the relationship $D = (\ln SL - \ln 7.2843) / 0.0280$ (Muth 1990). An estimated 50 adults inhabit a warm spring complex near RK 48; these fish are about 50 km upstream of the LCR and are likely remnants of a mainstem population that inhabited Grand Canyon prior to Glen Canyon Dam.

Evidence of successful reproduction in this area was also reported by Arizona Game and Fish Department (1994); 20 YOY (20–50 mm TL) chubs were collected from a backwater near President Harding Rapid (RK 71) in 1993. These and other juveniles reported from this area (Suttkus and Clemmer 1977, Carothers and Minckley 1981) likely hatched from eggs deposited in these warm springs, since other warm suitable spawning habitats have not been identified in the area. Furthermore, these fish were 32–48 km upstream of the only known spawning area, the LCR, and it is unlikely these young fish could swim this distance upstream.

Age and Growth

Average lengths of mainstem subadults at 1, 2, and 3 years, based on back-calculations from scale annuli, were 96, 144, and 186 mm TL, respectively. The majority of growth in the first year occurred in the LCR, since scale checks, indicating disrupted growth when the fish moved from the warm LCR to the colder mainstem, showed fish averaged 74 mm TL at time of descent; minimum size was 52 mm TL, indicating little or no survival of smaller fish descending from the LCR. The most likely cause of mortality was thermal shock or predation illicited by aberrant thermal-shock behavior, i.e., erratic swimming and flashing. Although no previous growth data were available for mainstem chubs, Kaeding and Zimmerman (1983) reported first scale annulus formation at 100 mm TL for LCR fish and 3-year-old fish were 250–300 mm TL.

Average length of females (n = 599) was 355 mm TL (range = 200–480) and average length of males (n = 623) was 338 mm TL (range = 202–460). Average weight of females was 454 g (range = 85–1,165) and average weight of males was 375 g (range = 43–1,122). These field observations indicate both males and females in Grand Canyon mature at about 200 mm TL or 3 years of age.

A logarithmic relationship (Von Bertalanffy 1938, Ricker 1975) was used to describe growth of chubs in the mainstem and LCR (Fig. 6). Mainstem growth rates were based on scale back-calculations for ages 0–3 and recaptured PIT-tagged fish for ages 4+. Assuming a length of 7 mm at hatching (Muth 1990), annual growth increments for 1, 2, and 3 years were 89 mm (7 to 96 mm TL), 48 mm (96 to 144 mm TL), and 42 mm (144 to 186 mm TL), respectively. Average 30-day growth rates were 10.3 mm (7 to 74 mm TL) for fish in the LCR, and 4.0 and 3.5 mm for 2 and 3-year olds, respectively, in the colder mainstem. Lupher and Clarkson (1994) reported average 30-day growth of laboratory chubs of about 2.3 mm at 10°C and about 10.6 mm at 20°C. The 30-day growth rate of 10.6 mm is comparable to 10.3 mm determined for the LCR fish from this study, but the higher rates of 4.0 and 3.5 mm for mainstem fish (compared to 2.3 mm) may be attributed to wild fish spending time in warm shallow shorelines or backwaters.

Average 30-day growth rates of recaptured PIT-tagged fish by 50-mm increments in the mainstem were 2.3 mm (150–200 mm TL), 2.8 mm (200–250 mm TL), 2.5 mm (250–300 mm TL), 1.2 mm (300–350 mm TL), 0.8 mm (350–400 mm TL), and 0.9 mm (>400 mm TL). Average growth rate of PIT-tagged fish in the mainstem was 16.6 mm per year. By comparison, average 30-day growth rates of chubs from the LCR (Minckley 1992) were 1.4 mm (<200 mm TL), 1.3 mm (200–250 mm TL), 1.1 mm (250–300 mm TL), 0.4 mm (300–350 mm), 0.5 mm (350–400 mm), and 0.1 mm (>400 mm TL). Average growth for all sizes and ages of LCR fish handled by Minckley was 13.5 mm per year. These results show growth rates of juveniles are higher in the seasonally-warmed LCR than in the mainstem, but higher for adults in the mainstem. This difference may be related to differential food availability between rivers and limited space in the LCR for adults (Valdez and Ryel 1995).

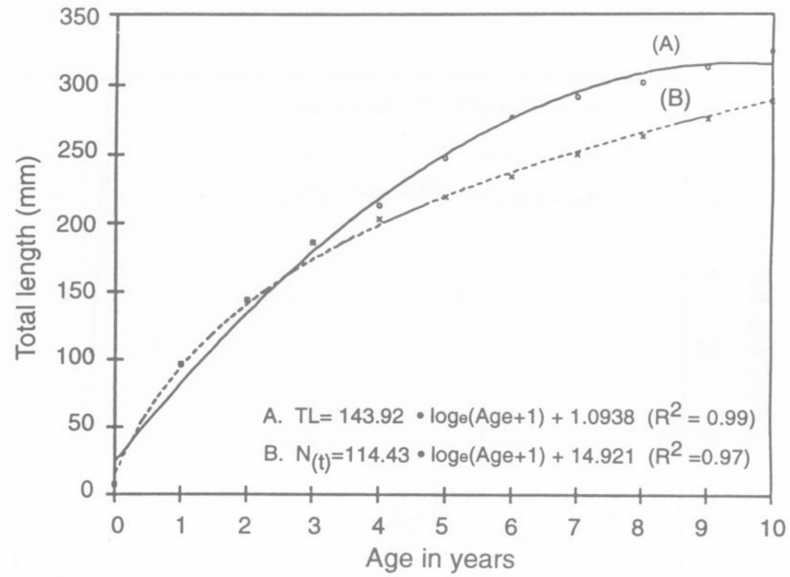


Fig. 6. Logarithmic growth curve for humpback chubs in the mainstem Colorado River (A) and in the Little Colorado River (B). Hatching length of 7 mm (Muth 1990) assumed. Length at 1–3 years from scale back-calculations; lengths at 50 mm increments for 4+ years from PIT tag recaptures. Growth curve for humpback chub in the LCR from Minckley (1992).

Survival

Mean monthly electrofishing catch rates (CPUE) for subadult humpback chubs (<200 mm TL) along mainstem shorelines (excluding backwaters) from the LCR to Hance Rapid in 1991, 1992, and 1993 peaked at 16.0, 15.5, and 52.2 fish/h, respectively. Successive decreases in densities are described as negative exponentials (Z_t; Ricker 1975), which showed similar semiannual survival rates of 0.31 and 0.33 for 1991 and 1992, respectively, but only $1x10^{-4}$ for 1993 (Fig. 7). Estimated annual survival rates were 0.10, 0.11, and

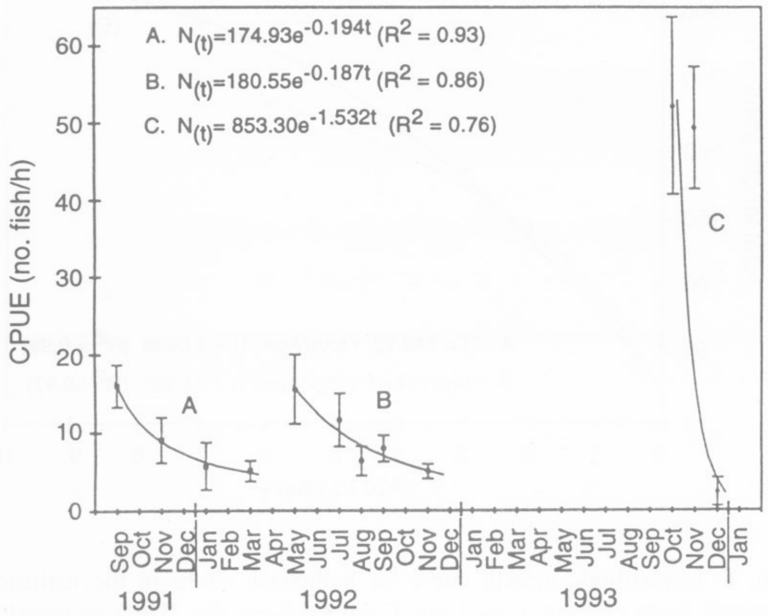


Fig. 7. Exponential decreases in densities of subadult humpback chubs in the Colorado River from the Little River confluence (RK 99) to Lava Canyon (RK 105) for September 1991 through March 1992 (A), May through November 1992 (B), and September through November 1993 (C).

1×10^{-8}, respectively. The average annual survival rate of adults during 1991–1993, using Jolly-Seber model estimators (Brownie et al. 1985), was 0.93 (95% CI = 0.89–0.97).

The main source of young chubs to the mainstem during our study was the LCR, with peak numbers descending during monsoon-induced freshets from May through September. Densities and distributions of subadults downstream of the LCR indicate some young fish dispersed to downstream aggregations. However, based on survival rates of subadults between the LCR and Hance Rapid and small numbers of subadults in other downstream aggregations, survival of young in the mainstem was low. Possible causes of mortality were identified as predation, starvation, and thermal shock.

Habitat

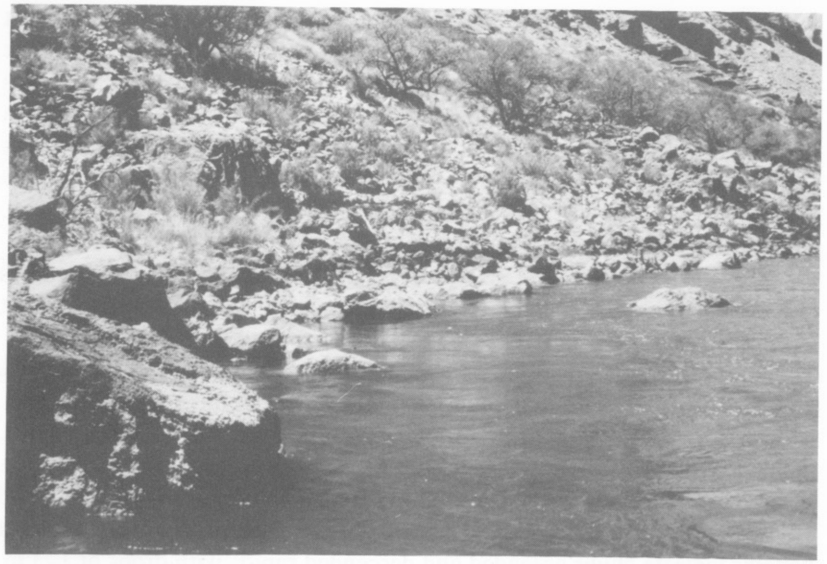
Most subadult chubs in the mainstem were along shorelines and most adults were offshore. An apparent transition in habitat use occurred with size and age, such that subadults moved from shoreline to offshore habitats beginning at about 1 year of age and ending at about 3 years of age, when fish reached maturity at 180–200 mm TL. Electrofishing CPUE of subadults was significantly higher (ANOVA, $P = 0.05$) in shorelines with vegetation (3.0 fish/h), talus (1.7 fish/h), and debris fans (0.9 fish/h) than those with bedrock, cobble, and sand (<0.5 fish/h) (Fig. 8).

The majority of adults in the mainstem were in large recirculating eddies (88% of adults captured and 74% of radio contacts), which comprised about 21% of surface area in the 13.5-km subreach sampled near the LCR inflow. Smaller percentages of adults were captured or radio-contacted in runs (7% and 16%, respectively) that comprised an average of 56% of surface area. Conversely, return channels, which were less than 1% of surface area, accounted for 4% of captured adults and 7% of radio contacts. Small numbers of adults (<1%) were also captured or contacted in pools and riffles, and although fish were neither caught nor radio-contacted in rapids, movement patterns indicate chubs ascended and descended rapids with drops of 1–3 m. Selection of eddy complexes may be related to use of low velocity habitat and greater food availability from entrainment of suspended material (Fig. 9). Relatively small movements in all seasons are attributed to proximity of feeding, resting, and cover habitats within small reaches of river. We found a consistent relationship between frequency and occurrence of debris fans, which form eddy complexes, and occurrence and numbers of adult humpback chub in Grand Canyon.

Food Habits

Gut contents of 168 adult chubs were collected with a stomach pump during 1991–1993. Of these, 10 (5.9%) had empty guts and were not included in the analyses. Of the remaining 158 fish, Simuliidae (blackflies), Chironomidae (midges), and *Gammarus lacustris* (freshwater amphipods) were in 78%, 58%, and 51% of guts, respectively. Other aquatic invertebrates, including Cladocera (water fleas), Neuroptera (spongillaflies), and Trichoptera (caddisflies) were found in 20%, 6%, and 5%, of guts, respectively. The most common terrestrial invertebrates were Hymenoptera (primarily ants), Coleoptera (beetles), and Diptera (true flies), which were in 21%, 15%, and 11% of guts, respectively. Hemiptera (true bugs), Orthoptera (grasshopper, crickets), and Homoptera (cicadas) were in 3%, 2%, and 2% of guts, respectively.

The composite volumetric diet of adults sampled near the LCR (n = 128) (excluding the green algae *Cladophora glomerata*) consisted of *G. lacustris* (45%), Simuliidae (40%), terrestrial invertebrates (9%), Chironomidae (5%),



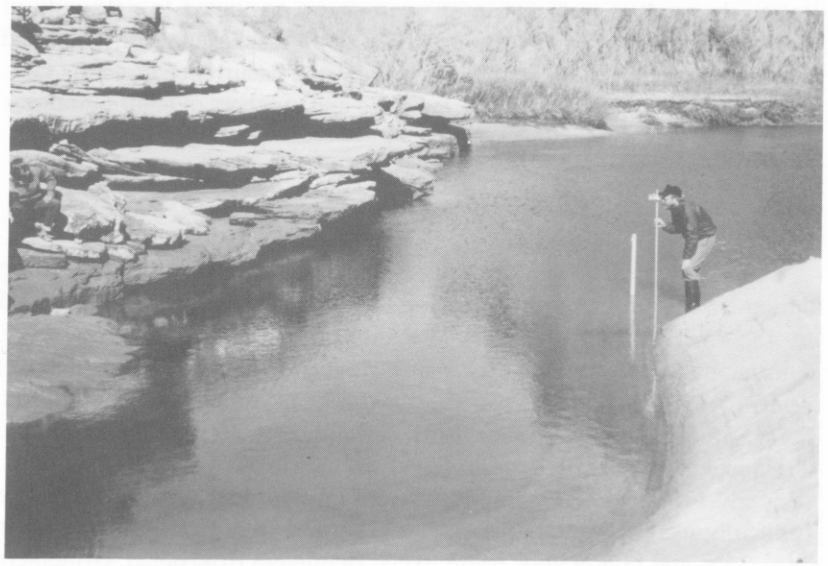


Fig. 8. Talus shorelines (top) and eddy return channels or backwaters (bottom) used by subadult humpback chubs in the Colorado River in Grand Canyon.

Fig. 9. The Colorado River in Grand Canyon about 127 km downstream of Glen Canyon Dam. Large lateral debris fans form recirculating eddies used by adult humpback chubs and associated sand bars.

and other aquatic invertebrates (1%) (Fig. 10); *C. glomerata* was found in 22% of chubs examined and comprised 23% of gut content volume. The diet by volume of adults from a more downstream aggregation in Middle Granite Gorge (MGG, $n = 24$) comprised of Simuliidae (49%), terrestrial invertebrates (30%), *G. lacustris* (10%), Chironomidae (5%), and other aquatic invertebrates (6%); *C. glomerata* was not present in guts of these fish. The high incidence of Simuliidae in gut contents was consistent between the LCR and MGG aggregations. Notable differences in diet between the two aggregations included a higher incidence of *G. lacustris* and *C. glomerata* in the LCR aggregation and a higher incidence of terrestrial invertebrates in the MGG aggregation. These results suggest terrestrial invertebrates become increasingly important to chubs in downstream reaches of Grand Canyon where aquatic food supplies are correspondingly lower.

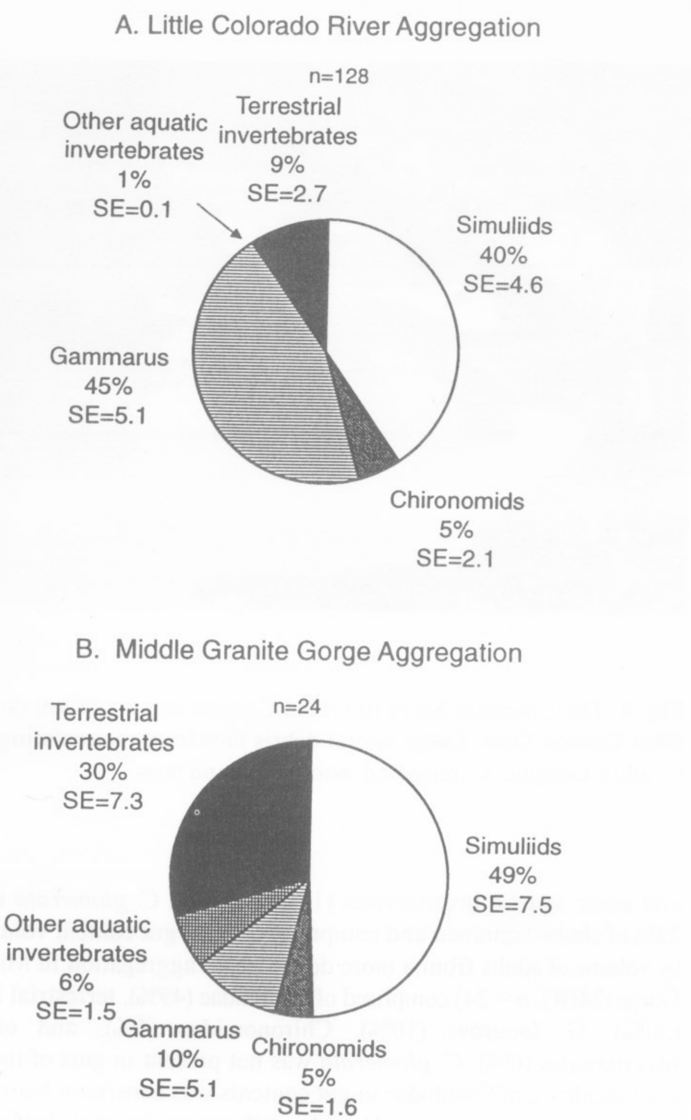


Fig. 10. Diet by volume of mainstem adult humpback chubs from near the Little Colorado river (A) and Middle Granite Gorge (B) during 1992–1993.

Predation

Of 328 stomachs taken from nonnative fishes in Grand Canyon in 1990–1993, only 6% contained fish remains and only two species--brown trout and channel catfish--contained remains of humpback chub. Of 48 brown trout, 9 (19%) contained remains totaling 15 fish, and 5 (10%) contained in total 10 humpback chub; 1 brown trout contained 4 chubs. Brown trout preying on chubs were 393–500 mm TL, and ingested chubs were 78–130 mm SL (mean = 95). Brown trout with ingested chubs were caught between RK 92 and RK 105, above and below the LCR inflow (RK 99).

Five of 68 (7%) channel catfish examined contained remains of 8 fish, including 1 humpback chub (95 mm SL), 1 bluehead sucker (*Catostomus discobolus;* 150 mm SL), 1 flannelmouth sucker (*C. latipinnis*; 170 mm SL), 1 unidentified sucker, and 4 unidentified fish. The catfish with the chub was 475 mm TL, and was captured at RK 99, immediately below the LCR inflow. Predation of humpback chub by channel catfish was also reported in the LCR by Arizona Game and Fish Department (C.O. Minckley, personal communication) and Arizona State University (M. Douglas, personal communication).

These findings indicate a population of 3,000 adult brown trout in Grand Canyon could consume approximately 227,760 subadult chubs annually and a population of 200 adult channel catfish could consume approximately 1,095 subadults annually. One unidentified fish was found in stomach contents of 163 rainbow trout (<1%). The dominance of invertebrates and algae and the absence of fish reflect the typical diet of rainbow trout in Grand Canyon (Maddux et al. 1987, Leibfried 1988). Of 39 striped bass (mean = 453 mm TL, range = 315–857 mm TL) captured in regions II and III, four (10%) contained remains of seven fish, including three trout and four unidentified fish. Striped bass may prey on humpback chub in Grand Canyon, but the magnitude of predation is probably small because of small numbers involved in annual spawning runs from Lake Mead (17 captured in 1991, 3 in 1992, and 19 in 1993) and the likelihood that these fish fast during spawning migrations (Stevens et al. 1987).

Parasites

The only external parasite on humpback chubs from the mainstem was the parasitic copepod, *Lernaea cyprinacea*. Eight of 6,294 (<1%) chubs were infected with an average of 1.25 copepods per fish (range = 1–2). None of the infected fish showed signs of stress or illness, although small open lesions were common at attachment sites. Valdez et al. (1982) reported this parasite on 26% of 234 humpback chubs from the upper Colorado River; it was not on YOY, but 17% of juveniles, and 31% of adults were infected with 1–13 copepods.

We attribute the low incidence of *L. cyprinacea* in Grand Canyon to persistent suboptimal mainstem temperatures. The favorable temperature range for this parasite is 14–32°C; temperatures outside of this range prevent hatching and transformation of female larvae (Shields and Tidd 1968). Although maturation occurs in 15 days at 30°C (Stoskopf 1993), the parasite is unable to complete its life cycle at temperatures below 14°C, pH below 7.0, and salinity at or above 1.8% (Hoffman 1976). Copepods have been observed parasitizing fish only when water temperature exceeds 25°C (Marcogliese 1991); hence, infection by this parasite probably occurs primarily in warmed tributaries and persistently warm habitats, such as long-lived backwaters or marshes.

The only internal parasite observed in chubs during this study was the Asian tapeworm, *Bothriocephalus acheilognathi*, which was in the gut of 6 of 168 (4%) adults flushed with a stomach pump and averaged 6.7 tapeworms (range = 1–28) per infected fish. Because the stomach pumping technique may not be effective at flushing this tapeworm from the gut of fish, this reported frequency and intensity of infestation may be an underestimate. Subadult chubs were not examined internally or subjected to stomach flushing.

Asian tapeworms were first reported in humpback chubs from Grand Canyon in 1990 (D. Hendrickson, personal communication). Angradi et al. (1992) reported this parasite in 80% of juveniles (range = 13–35 mm TL) from the LCR in 1990, but none in 1989. Asian tapeworms were first reported in North America in 1975 in golden shiners (*Notemigonus crysoleucas*) and fathead minnows (*Pimephales promelas*) and in the United States in grass carp (*Ctenopharyngodon idella*) (Hoffman 1976). The primary host is one of several species of cyclopoid copepods, and the principal adult hosts are members of the minnow family, although it has also been found in non-cyprinids in Asia and Europe (Babaev 1965, Bauer et al. 1969), where it is considered a dangerous fish parasite. Asian tapeworms can grow to 100 mm long and 2 mm wide with a large triangular scolex or head, which is characteristic for the species.

Temperature has a significant effect on maturation and growth of *B. acheilognathi* (Granath and Esch 1983). Maximum egg hatching and development of all life stages occurs at 30°C, although stimulation for growth, development, and maturation of eggs occurred above 25°C. Highest densities of tapeworms were found at 20°C (temperatures below 20°C were not tested). Thus, while this parasite can live in fish at mainstem temperatures, full development and infection of other fishes can occur only in persistent warm habitats with appropriate primary hosts.

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